

Life-habits and Infaunal Posture of *Cumingia tellinoides* (Tellinacea, Semelidae): An Example of Evolutionary Parallelism

by

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Abstract. The semelid clam *Cumingia tellinoides* is an infaunal burrowing form found in sandy organic deposits. Its eggs have been used in experimental embryology for over 80 years, and it has usually been reported to have a vertical life-posture and a "nearly equivalve" shell. In populations from the Cape Cod area, the majority of individuals live and feed while lying horizontally within the sediment and show asymmetries of shell structure. Observations and photographs of movements and feeding postures were made possible by use of artificial substrates prepared from cryolite.

There is considerable individual plasticity of behavior and shell variation in *Cumingia tellinoides*. For all field and laboratory observations, 76.1% of individual clams were found lying on one shell valve (and in 78.4% of these it was the left valve down). Some corresponding deformation of the posterior shell margins was found in 79.2%, and in 42.9% this amounted to a clear lateral twist (in 65.4% of these to the right, or posturally upwards). Internal asymmetries of the pallial sinus were found in 60.8% of shell valve pairs, and there was a significant ($P < 0.05$) inverse correlation between lateral twist direction and larger sinus scar areas in *Cumingia tellinoides*. In contrast, in the sympatric tellinid clam *Macoma tenta*, all were found lying on their left valves, all shells showed a right-handed twist, and 93.7% had a larger area in the left pallial sinus.

The pattern of horizontal feeding posture, associated with posterior twisting and asymmetric pallial lines in the shell valves, appears to be variably expressed in *Cumingia tellinoides*, contrasting with similar but obligate features in *Macoma tenta*. It seems most probable that the occurrences of horizontal life-style (and associated asymmetries of shell and muscles) in both semelid and tellinid lineages constitute an example of evolutionary parallelism rather than of evolutionary convergence.

INTRODUCTION

LITTLE HAS BEEN published on the natural history of the semelid clam *Cumingia tellinoides* Conrad despite extensive laboratory use of its eggs as material for experimental embryology for over 80 years. In general, within the burrowing and infaunal superfamilies of lamellibranchs, an inequivalve condition of the bivalve shell is associated with a non-vertical posture in the substrate. More than half of the species in the Tellinidae, and a number of species in the Semelidae, are known to have a twist (usually to the

right) of the posterior margins of their shell valves. Earlier surveys of the life-habitats of such infaunal bivalves (STANLEY, 1970; ABBOTT, 1974) claimed a vertical life-posture and a "nearly equivalve" shell for *Cumingia*.

We now report that, in *Cumingia tellinoides*, the majority of individuals live and feed while buried nearly horizontally in the sediment, and many show not only a slight posterior twist to the shell valves but also an internal asymmetry of the scars of the pallial sinus (that is, of the attachment of the siphonal retractor muscles to the shell valves). Use of artificial deposits made from the pure mineral cryolite allowed us to obtain photographs of living specimens of *C. tellinoides* in their feeding posture within the substrate (some reproduced here). These observations and results are discussed in relation to other molluscan

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examples of parallelism and convergence in adaptation. Critical assessment of cladistic systematics has re-emphasized the need for discrimination between convergence and parallelism (MAYR, 1974), and this is partly responsible for a revival of interest in such evolutionary distinctions at all levels of biological organization.

MATERIALS AND METHODS

In the Cape Cod area, *Cumingia tellinoides* lives in sandy organic deposits associated with eelgrass (*Zostera*), around the level of MLWST and for about 20 cm deeper. More specifically, it is found in fine sand with a high fraction of peaty material and sometimes even among eelgrass roots, not usually under the densest beds of *Zostera*, but rather where there are sparser clumps of eelgrass along the margins of the little channels that drain the flats during the lowest tides (GRAVE, 1927; and author's observations). Healthy specimens used for measurement and photography were collected on various occasions between 1973 and 1981 from an area of flats in the Northwest Gutter of Hadley Harbor (in the Elizabeth Islands, near Woods Hole). Populations of *C. tellinoides* have also been examined in the other gutters of the Hadley system, and in similar microhabitats in the tidal harbors of North Falmouth, Quisset and Orleans, all on Cape Cod. From about 1907 to 1927, *C. tellinoides* was collected regularly and intensively to provide eggs for embryologists and cell-physiologists (including H. E. Jordan, E. G. Conklin, F. R. Lillie, E. Browne-Harvey, B. H. Grave, T. H. Morgan, and L. V. Heilbrunn) working in the Marine Biological Laboratory at Woods Hole. It apparently became a very rare species with the decline of eelgrass beds between 1930 and 1960, but was listed normally and not marked as "rare" in a faunal key prepared in 1963 (RUSSELL HUNTER & BROWN, 1964). It is now (1980-83) not uncommon again, although limited to certain localities and to the highly specific microhabitat described above.

The family Semelidae, in which the genus *Cumingia* is placed along with *Semele* and *Abra*, can be separated from the family Tellinidae (including *Tellina* and *Macoma*) by major differences in the functional shell ligament and in hinge dentition. These features of shell morphology will be discussed more fully below, but it should be noted that *Cumingia* (like all semelids) has an internal resilium (carried on a chondrophore plate) as its functional shell ligament, while all tellinids, including those local species of *Macoma* which can be nearly sympatric (*Macoma tenta* and *M. balthica*), have elongate external ligaments.

Observations and photographs of the movements and feeding posture of *Cumingia tellinoides* within the substrate were made using artificial deposits ground and sieved to size from large pure crystals of the mineral cryolite, which has a refractive index close to that of seawater. Biological application of this material was first described by JOSEPHSON & FLESSA (1971, 1972), and its use for

these studies on *Cumingia* reported in an abstract (RUSSELL-HUNTER & TASHIRO, 1973). Cryolite media are better suited for invertebrates such as *Cumingia* that live in sand deposits, being more resistant to penetration than are those prepared from methylcellulose (HUNTER, 1982; HUNTER *et al.*, 1983) which are better for worms from flocculent mud deposits. When suitably illuminated, granular cryolite in seawater is relatively "transparent," permitting close observations of pedal and siphonal movements within the substrate and allowing photography at moderately high resolution.

Each experimental aquarium was prepared by clamping two sheets of plate glass (approximately 20 cm square) around a piece of thick-walled rubber hose (of 1.5 or 2.8 cm outside diameter) bent into a U-shape, and filling the U to a depth of 8 to 10 cm with field-collected natural substrate or with ground cryolite in about 15 cm of seawater. Photographs were taken with a 105-mm lens and bellows on a Bronica (6 cm square) camera, using Kodak Plus-X film rated at ASA 210 and developed in half-strength Acufine. Most photographs were taken with both front (direct) and back (transmitted) lighting of the substrate. The results (see Figures 1, 4, 6) show edge definition and resolution somewhat better than those achieved using X-radiography by STANLEY (1970) in the course of his heroic survey of the life habits of 98 extant bivalve species.

OBSERVATIONS AND RESULTS

During the summers from 1961 to 1972, the frequency with which *Cumingia tellinoides* appeared in field collections of the Invertebrate Zoology course at Woods Hole increased. In 1967 and 1968, casual inspection of samples totaling about 25 animals each year revealed that the majority showed some deformation of the posterior margins of the shell valves, with many showing a definite posterior twist as in Figure 3. Casual observations of live *C. tellinoides* in the same two years showed that the majority lay on one side in the sediment as did the more abundant *Macoma tenta*.

There is obviously some individual plasticity of behavior in *Cumingia tellinoides*. During a more intensive study in 1973, in the course of several burrowing experiments, a total of 51 specimens was left each for just over 48 h in dishes with about 6 cm depth of natural sediments freshly collected from the field. To describe orientation, we can use the sagittal plane of each individual clam (that is, the plane defined by both the antero-posterior and dorso-ventral axes which, in symmetrical bivalves, is also the plane where the edges of the shell valves meet on adduction). Of the 51, 7 (13.7%) had their sagittal planes vertical and thus could be actively burrowing, while 5 (10%) had their sagittal planes at about 45° to the surface of the sediment. The majority (39/51 or 76.5%) lay with their sagittal planes nearly horizontal (that is, parallel to the sediment surface). Shell-lengths of this group ranged from

9.0 to 17.8 mm (mean 12.6 mm) and, for those lying horizontal in the sediment, the average depth of burial was about 15 mm or just over one shell-length. In the field, living specimens of *C. tellinoides* are usually found buried at depths of about twice their individual shell-lengths. For 16 specimens carefully uncovered by finger in the field, none had vertical sagittal planes, and only 4 approached 45° from the horizontal. Both in the laboratory dishes and in the field, most horizontal specimens of *C. tellinoides* lay on their left side, but a few lay on their right (see shell proportions below). This contrasts with conditions in adjacent populations of the tellinid *Macoma tenta* where the feeding posture of every individual is lying on its left valve (which is somewhat more convex).

Many tellinids, which take up a horizontal feeding posture within the substrate, burrow relatively rapidly from the surface with their sagittal planes at a low angle from the horizontal (HOLME, 1961; STANLEY, 1970). For each species studied in detail, an obligate orientation has been reported. In contrast, individuals of *Cumingia tellinoides* burrow rather slowly, and enter both natural sediments and cryolite deposits with their sagittal planes at a slight angle to the vertical (Figures 1, 2). The dorsal or hinge side is characteristically lower, but the slight lateral inclination that is normal may be to either the left or the right side. Burrowing is essentially similar to that in unspecialized and more globose bivalves (ANSELL & TRUEMAN, 1967; TRUEMAN, 1968; TRUEMAN *et al.*, 1966), with alternate *points d'appui* being provided by the opening gape of the shell valves and the dilatible foot. Some feeding can go on during parts of the burrowing cycle (Figure 1). At a depth corresponding to shell length, the lateral inclination increases and the sedentary posture (nearly horizontal) is taken up. Figures 4, 5, and 6 show specimens with siphons extended for feeding. Once this posture is established the foot is rarely extended, and it is likely that, in the peaty sand substrates of the field, *C. tellinoides* does not move much once established in the substrate. A number of earlier authors including STANLEY (1970) have claimed a vertical posture for *C. tellinoides* when feeding, and one X-radiograph in his survey shows four specimens all anterior down and vertical with siphons extended in feeding, with channels in the substrate revealing former siphon positions. It seems possible that the individual plasticity of behavior (including infaunal posture) in *C. tellinoides* could involve different norms for different populations, perhaps with some relation to different substrate conditions.

In all of our observations (including the clams of Figures 4, 5, and 6) the inhalant (ventral) siphon was directed nearly vertically and was used in both suspension and deposit-feeding, while the exhalant (dorsal) siphon discharged below the surface or reached it at an obtuse angle at least 10 mm away from the inhalant. With healthy animals in cryolite deposits, it is easy to distinguish the small spherical fecal pellets and the larger, somewhat less consolidated, masses of pseudofeces as they move within

the extended siphons. Only true feces are discharged through the exhalant siphon, they pass slowly but regularly into the substrate, either (Figure 4) close to the dorso-posterior shell margin with little siphonal extension, or (Figures 5, 6) in a wide arc posteriorly and upward. Similar discharge of the exhalant siphon within the substrate has been reported for the tellinids *Macoma nasuta* (MACGINITIE, 1935) and *Arcopagia crassa* (HOLME, 1961). At irregular intervals the larger softer masses of pseudofeces are shot vertically up the inhalant siphon high above the sediment surface (as a result of partial valve adduction). [It should be noted that, in Figure 4, a fecal pellet shown halfway to the surface is *not* inside the inhalant siphon.] More frequent discharge of pseudofeces (in somewhat larger, looser masses) occurs during periods of deposit-feeding. This flexibility of feeding behavior found in *Cumingia tellinoides* is probably unusual in semelid and tellinid bivalves since most investigators (YONGE, 1949; HOLME, 1961; STANLEY, 1970; ABBOTT, 1974) suggest that each species in these two families is either a suspension feeder or a deposit-feeder. However, BRAFIELD & NEWELL (1961) have claimed that certain British populations of *Macoma balthica* show tidally controlled alternation of suspension- and deposit-feeding. For the same species in Denmark, RASMUSSEN (1973) has illustrated both feeding modes. However, GILBERT (1977) regards it as an obligatory deposit feeder, while TUNNICLIFFE & RISK (1977) conclude that it must supplement its protein intake by suspension-feeding when submerged.

Figure 7 is a vertical photograph of the inhalant siphon of a specimen of *Cumingia tellinoides* living in natural substrate and engaged in deposit-feeding. Despite the quality of the photograph (poor contrast, and little depth of focus), some radiating marks can be detected on the surface of the sediment. These are in conformity with our observations that, during deposit-feeding the recurved inhalant siphon of *C. tellinoides* is not swept in a circular path as is the case in most deposit-feeding tellinids (YONGE, 1949; HOLME, 1950, 1961; STANLEY, 1970), but sucks in a series of radial skimming movements directed centripetally (like *Macoma tenta*; STANLEY, 1970). Rejection of pseudofeces commonly occurs after each group of three or four radial sweeps.

Three collections of *Cumingia tellinoides* totaling 79 individuals were used to quantify shell variation. Most of these were killed by immersion in hot water and subsequent removal of the soft tissues, but 17 clams had initially been fixed in formalin. Of the total, 2 were damaged in preparation and 3 others were too small for assessment of the pallial sinus, so that shell features are reported for 77 shell-valve pairs (or 74 pairs for sinus asymmetries). Some deformation of the posterior part of the shell was found in one or both valves of 61/77 or 79.2%, and this amounted to a clear twist (as in Figure 3) in 33/77 or 42.9%. In a few cases, a twist to the left had been preceded by a twist to the right, or vice versa, and in two sets of valve pairs a series of alternate "twists" seemed to have oc-

curred. Of these with a single clear twist, 9/26 turned left while 17/26 turned right. This figure of 65.4% with the posterior shell margins turned right (corresponding to growth during a sedentary period of infaunal posture lying on the left valve) is considerably less than the figure of 78.4% for clams found alive lying on their left valves (as a percentage of the combined numbers for all live field and laboratory observations found lying horizontally, which amounted in turn to 76.1% of all observations). In other words, although left valve down occurs in a majority (59.7%) of our live observations, the corresponding shell twist is found only in a plurality (22% single clear, or 28.6% total) of shell pairs studied.

Another asymmetry shown by the shell-valve pairs, which may be of considerable functional importance, concerns modification of the internal attachment of the siphonal retractor muscles. These so-called pallial sinus scars form embayments of the pallial lines, which elsewhere run concentric with the shell margins and mark the insertion in the nacreous layer of the shell for the line of muscles from the innermost of the three lobes of the mantle edge. Asymmetries between left and right shell-valves of the pallial sinus scars can involve (a) the areas enclosed by the scars (reflecting the "spread" of the muscle attachments), (b) the width of the scar lines (reflecting the thickness of the attached muscle sheet), or (c) the shape of the sinus embayment ranging from broadly ovate to triangular. This third kind of asymmetry is less easily quantified. One or more of these three asymmetries were found in 45/74 or 60.8% of the shell-valve pairs. Once again there were biases of orientation but no uniformity of handedness. The scar area was larger in 19 left valves and in 14 right valves, and the scar was more pronounced in 8 left valves and in 14 right valves. There was a tendency for

those shells with the posterior margins twisted to the right (being the plurality) to show larger scar areas in the left valve and more pronounced scar lines in the right valve, while the shells with a left-handed twist (the minority) tended to show the opposite conditions. In a 3×3 contingency table, there was a significant inverse correlation between marginal twist direction and larger sinus scar areas (summed chi-squares = 10.667, df 4, $P < 0.05$). For comparison, in a sample of *Macoma tenta* totaling 63 individuals, all shells showed a right-handed twist which could involve more than one third of the length of the shell, and 59/63 or 93.7% showed a larger pallial sinus area in the left valve. Clearly in *Cumingia tellinoides* those shell asymmetries related to infaunal posture show levels of individual variation that parallel the individual plasticity of behavior.

DISCUSSION

The fact that *Cumingia tellinoides* is found in a marginal microhabitat is relevant to any discussion of the variable behavior exhibited by individuals and of the related asymmetries of their shells.

Two principal life-styles are found in the bivalve sub-order or superfamily Tellinacea. Some species and genera show a capacity for rapid reburrowing associated with symmetrical, streamlined, smooth shells, and those may live in shifting substrata or move laterally in a near horizontal orientation in the course of deposit-feeding (HOLME, 1961; STANLEY, 1970). Other, often closely related, species are less typically members of the mobile "superficial in-fauna," seem adapted for a more permanently sedentary way of life, and may live in peaty deposits or among the root systems of eelgrass (*Zostera*) or turtle-grass (*Thalass-*

Explanation of Figures 1 to 7

Figure 1. An early stage in burrowing in an adult specimen of *Cumingia tellinoides* (12.8 mm shell length), with some feeding continuing through the open siphons. The photograph was made in an artificial deposit of ground and sieved crystalline cryolite (as were Figures 2, 4, 5, and 6).

Figure 2. The same clam as in Figure 1 a few seconds later, with the dilatable foot being extended and the siphons closed.

Figure 3. Dorsal view of the posterior margins in an adult shell of *Cumingia tellinoides*. The right shell valve is above, and the scale-bar equals 1 mm.

Figure 4. Sedentary feeding posture of an adult specimen of *Cumingia tellinoides* (13.3 mm), photographed in cryolite with the dorsal (hinge) side toward the camera, showing the inhalant siphon extending vertically to the surface. [Note that the fecal pellet halfway to the surface is *not* inside the siphon.]

Figure 5. Feeding posture in another (11.9 mm) specimen viewed from the ventral side. Three fecal pellets have been deposited by the downturned exhalant siphon close to the posterior shell margin.

Figure 6. Ventral view of the feeding posture in another (14.6 mm) specimen. This clam is engaged in suspension-feeding rather than deposit-feeding. Fecal pellets have been deposited in an arc up to the surface of the deposit by the exhalant siphon which is extended horizontally in the photograph.

Figure 7. Vertical photograph of the inhalant siphon of a specimen of *Cumingia tellinoides* living in natural substrate. The faint radial marks to the right of the siphon represent tracks of recent inhalant passes during deposit-feeding. The scale-bar equals 2 mm.



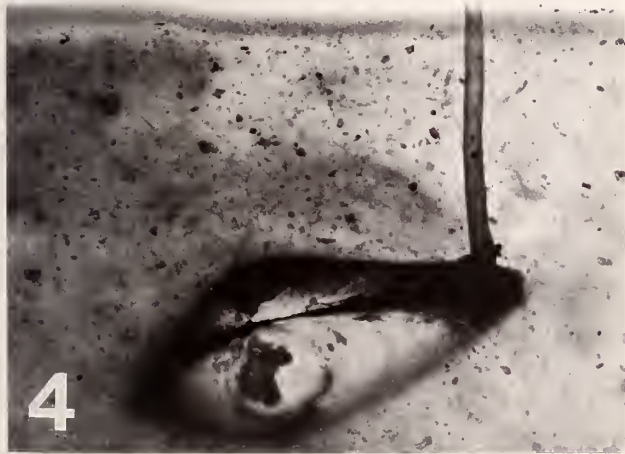
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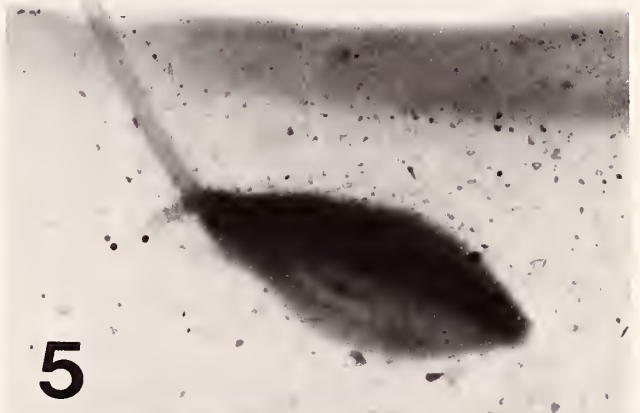
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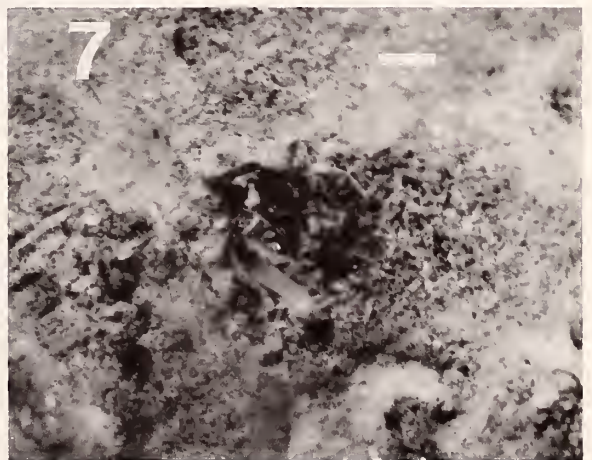
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sia). Despite statements by some authors, there is no universal correlation of the first life-style with deposit-feeding and the second with suspension-feeding. Asymmetries of the shell valves of adults (including the posterior marginal twist, and inequalities of the pallial sinus) are clearly associated with a horizontal infaunal habit (*i.e.*, lying on one shell valve), and increased functional efficiency in that posture. However, it now appears that either life-style (rapid-reburrowing or sedentary) may be associated with a horizontal infaunal posture. Further, the results from this study of *Cumingia tellinoides* demonstrate that great individual shell variation and plasticity of behavior are possible within a species.

Features common to the four families of the Tellinacea include separate long extensible siphons, a blade-like foot for burrowing, a pallial cruciform muscle (GRAHAM, 1934; YONGE, 1949, 1957), and rather large labial palps. During deposit-feeding, the palps are used for sorting the detritus which is sucked in from the surface by a vacuum-cleaner-like action of the inhalant siphon (Figure 7). Within the superfamily, two of the families, the Tellinidae, to which the genera *Tellina* and *Macoma* belong, and the Semelidae, to which *Semele*, *Abra*, and *Cumingia* belong, can be separated by major differences of the functional ligament and hinge dentition. The tellinids have an elongate external ligament with rather weak teeth, while the semelids have an internal resilium as the functional ligament (carried on a chondrophore plate rather like that of *Mya*), and strong cardinal and lateral hinge-teeth. These are features regarded as phylogenetically sound and as genetically conservative by most systematists and paleontologists. This assessment need not be modified by the observations of TRUEMAN (1953, 1966) which suggest that the larger internal ligament of the semelids is homologous with the tiny cardinal ligament present temporarily in juveniles (spat) of some tellinids (*Macoma* and *Tellina*), and is therefore neotenic.

Cumingia tellinoides is frequently found living with *Macoma tenta* (although *M. tenta* is more widely found alone in bare muddy sands 3–8 m below MLWST). The habit of lying on one side in the sediment (as done by both species) and the structural asymmetries associated with the habit, must have evolved independently in semelids and tellinids. There are a number of other well-established cases of ecologically sympatric pairs of species derived from morphologically distinct stocks of bivalves. As discussed by MAYR (1969, 1974) and BOCK (1963, 1965) it is often difficult to distinguish cases of major evolutionary convergence from similarities in allied stocks which result from parallelism. Among bivalves, striking similarities of shell structure and muscle mechanics can be found in sympatric forms derived from widely different superfamilies—for example, fused-siphon deep-burrowers from both Myacea and Mactracea, globose ribbed cockles from Cardiacea and Arcacea, and borers in soft rock (*Hiatella*, *Petricola*, and *Zirphaea*) from three distinct superfamilies. These are almost certainly all cases of evolutionary con-

vergence as distinguished by MAYR (1969, 1974), as are the many and polyphyletic stocks of limpetlike gastropods (RUSSELL-HUNTER, 1982).

With the common features of infaunal posture and shell modification in *Macoma* and *Cumingia*, however, we may be observing the results of parallelism, or similarities of structure and function produced by shared genotypic features (not expressed in this combination in other related forms). In this view, some of the other features noted above as common to the overall group, the Tellinacea, are of paramount importance. These include the cruciform muscle (YONGE, 1949, 1957; see also GRAHAM, 1934), which may be involved in adjusting the basal attitude of the siphons, and also the mode of extension of the siphons (CHAPMAN & NEWELL, 1956; see also CHAPMAN, 1958) using radial muscles *within* the siphonal walls, so that water circulation and feeding can go on during a smooth and continuous process of protrusion. This is totally unlike the mechanism of siphonal extension employed in *Hiatella* (RUSSELL HUNTER, 1949) and in *Mya* (CHAPMAN & NEWELL, 1956) where protrusion occurs in stepwise stages involving *closed* siphonal tips and serial contractions of the shell adductor muscles. Along with these features common to the shared superfamily, the tellinid *Macoma* and the semelid *Cumingia* both exhibit structural features, such as the posterior shell twist and asymmetries of the pallial sinus, which may be correlates of a horizontal infaunal posture. Evolutionary hypotheses regarding such correlates must be based on analyses of function, and of adaptive significance, as clearly articulated by BOCK (1965, see also BOCK & VON WAHLERT, 1965) in discussing similar vertebrate cases. In considering all bivalve species in the Tellinacea (or all individuals in a variable species like *Cumingia tellinoides*), it is important to note that these correlates of structure with behavior are not reciprocal. All twisted shells occur in species (or individuals) that live in a horizontal infaunal posture, but not all forms living horizontally have shell twists.

The functional significance of the shell twist is clearly related to its molding of the siphonal bases and to the hydraulics of water circulation in feeding. MACGINITIE (1935) provided the earliest description of the implications of the horizontal posture for feeding behavior in *Macoma nasuta*, and this was built upon by HOLME (1961) in his observations on five British tellinid species with this life-style. It was left to STANLEY (1970) to illustrate and discuss the fact that an upward twist of the posterior valve margins (where the siphons emerge from the shell) serves to broaden the radius of siphonal curvature and streamline water flow. This can be seen in Figures 4 and 6, and it is obviously more important to the inhalant siphon with its near vertical orientation. Our observations on *Cumingia tellinoides* in cryolite confirm Stanley's functional analysis, but add the necessary discharge of pseudofeces through the *inhalant* siphon as a factor favoring streamlining of the bend in that siphon at the shell margin. As already noted, in the sympatric form *Macoma tenta* all individuals

lie horizontally on their left valves, and all show a right-handed posterior twist, which can extend over one-third of the length of the shell. [There is an intriguing possibility that mirror-image races of *M. tenta* may exist, because ABBOTT (1974) gives as specific characteristics "posterior and narrower end slightly twisted to the left."] However, unlike the variable conditions found in *C. tellinoides*, curvature of the shell in *M. tenta* is universal and seems to result from an obligate growth pattern which continues through most of adult life and results in the left valve being somewhat more convex than the right. This is carried even further in another bizarre tellinid, *Tellidora cristata*, which has an almost "oyster-like" arrangement of a flat left valve and a bowl-shaped right valve. Unfortunately, nothing is known about life-habits in *T. cristata*.

Two distinct life-styles have been associated with the horizontal infaunal posture. In active species like *Tellina tenuis* and *T. agilis*, HOLME (1961) and STANLEY (1970) claim that the horizontal posture facilitates lateral movements in the substrate within a single plane, thus maintaining an even depth of burial. In contrast, in some species of *Macoma* and in *Cumingia tellinoides* the horizontal posture is associated with more permanently immobile feeding habits and a relatively sedentary life-style. This is also the case for *Semele proficua*, which has a symmetrical discoid shell but lives horizontally on its left side among roots of *Thalassia*, and could also be predicted as the life-style of the extremely asymmetric *Tellidora*. To further complicate matters, several species of *Macoma* with marked asymmetry of the pallial sinus have no shell twist and have been listed in most general accounts (along with *C. tellinoides*) as having a vertical life posture and near equi-valve shells. General surveys of fossil faunas of bivalves show a majority of species to be infaunal (NICOL, 1968), and inequivalve representatives to occur in at least 28 families (NICOL, 1958; see also NEWELL & MERCHANT, 1939), but reveal no regularities of habit.

Given the variety of associations listed above for the Tellinacea, it seems most probable that the occurrences of horizontal life-style (and associated asymmetries of shell and muscles) in both tellinid and semelid lineages constitute an example of evolutionary parallelism. Although it makes no reference to shared genotypic features, an early definition by SIMPSON (1961) remains valid: "parallelism is the independent occurrence of similar changes in groups from a common ancestry and because they had a common ancestry." An earlier discussion of parallel adaptations in related stocks was set out by RENSCH (1943) along with other germinal ideas about evolution above the species level, and OSCHER (1965) gives more detailed analyses of the potentialities of "hidden" gene combinations. The importance of attempting to discriminate between evolutionary convergence and parallelism has been re-emphasized in the course of a critique of cladistic systematics (MAYR, 1974), and in relation to the debate on molluscan evidence for punctuated equilibria in evolutionary lineages (MAYR,

1982). The present example of parallelism provided by the pattern of variably expressed behavior and shell morphology in the semelid *Cumingia tellinoides*, and of similar but obligate features in the tellinid *Macoma tenta*, may permit future experimental investigation. Meanwhile, use of such features as asymmetry of the pallial sinus to deduce life-style or infaunal posture in stocks of fossil or extant bivalves is questionable.

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